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Correlations between Sequential Timing Decisions Do Not Necessarily Indicate Strategic Behavior: A Comment on Bêty et al.

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Introduction

A seasonal decline of reproductive success is a common phenomenon in many bird species. The most common explanation is a trade-off between parental effort and offspring survival, mediated by parent and offspring nutritional condition (e.g., Lack 1950; Perrins 1970; Daan and Tinbergen 1997). A parent bird's nutritional body condition is assumed to increase before the reproductive season, thus enabling the bird to allocate resources to lay eggs (if female) and to provide for offspring over the season (both sexes; Drent 2006). Food availability for offspring decreases over the course of the season, which leads to a decline of survival chances for offspring. Theory predicts a trade-off between the advantage of a longer prelaying period (better parent condition) and the advantage of early breeding (higher food availability for offspring; Drent and Daan 1980; Daan and Tinbergen 1997). This trade-off is thought to affect the strategic decisions determining the timing of birds' breeding seasons (Drent and Daan 1980).

In migratory birds, the onset of egg laying is constrained by the timing of arrival on the breeding grounds after spring migration (Both and Visser 2001; Drent et al. 2003). Timing of arrival, in turn, is constrained by environmental parameters but likely also by individual quality (Piersma 1987; Drent et al. 2003; Drent 2006). Therefore, the timing of the sequential temporal variables of reproduction (arrival, prelaying period, and timing of breeding) in relation to each other is a result of strategic decisions of migratory

birds to optimize reproductive output (for an overview, see Drent 2006).

In their article, Bêty et al. (2003) set out to test the condition-dependent model of optimal clutch size in a migratory bird. They examined whether early-arriving snow geese (*Chen caerulescens atlantica*) experience a longer delay (prelaying period = laying date – arrival date) on the breeding grounds but still lay earlier than late-arriving conspecifics, which they assumed would indicate that these birds adjust their timing of migration and reproduction to optimize fitness. They used Pearson correlation coefficients and linear regression to examine relationships between timing of arrival and nesting and length of the prelaying period (Bêty et al. 2003). They found that arrival date is strongly correlated with prelaying period and laying date (tables 1, 2 and fig. 5 in Bêty et al. 2003). Their conclusion is that “geese appeared to simultaneously adjust their lay date ... according to their ... migratory behavior in order to optimize their expected reproductive success” (p. 116). By October 7, 2010, this article had been cited 55 times (ISI Web of Knowledge). Other studies repeated similar analyses on different species, reaching similar conclusions (e.g., Hupp et al. 2006; Ely et al. 2007; Vergara et al. 2007).

In this commentary, we challenge the assumption that correlation or regression analyses of sequentially occurring timing decisions are sufficient to indicate strategic reproductive behavior, because the lack thereof does not necessarily lead to an absence of correlation between arrival, prelaying period, and laying date. We support this claim by testing for correlations between different sequentially occurring timing variables, without assuming any strategic decisions on the side of the individuals.

Analysis

We assume that arrival dates (*A*) and prelaying periods (*D*) are nonstrategic (i.e., the result of environmental con-

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straints) and are therefore drawn from two independent distributions. Then laying date (L) is the sum of A and D ($L = A + D$). We compute covariance (Cov) and correlation (Corr) between A or D and laying date L (see, e.g., Quinn and Keough 2002). The covariation between A and L is $\text{Cov}(A, L) = \text{Cov}(A, A + D) = \text{Var}(A) + \text{Cov}(A, D)$. If A and D are uncorrelated, then $\text{Cov}(A, D) = 0$ and $\text{Cov}(A, L) = \text{Var}(A)$. Therefore, since $\text{Var}(L) = \text{Var}(A) + \text{Var}(D)$,

$$\text{Corr}(A, L) = \frac{Sd(A)}{\sqrt{\text{Var}(A) + \text{Var}(D)}}.$$

Thus, the correlation between A and L is positive. This shows that A and L cannot be uncorrelated when assuming independence between A and D . The same logic can be applied to a situation where D is the result of environmentally imposed A and L , which results in a negative correlation.

Discussion

We show that even if individuals are not assumed to behave strategically, arrival date and laying date will often not be statistically independent. Clutch initiation in temperate- and arctic-breeding birds is naturally constrained by environmental variables like snow cover, temperature, and food availability, leading to a limited time period during which breeding and hatching can occur (Klaassen et al. 2006). Thus, the time period when egg laying can actually take place differs between individuals: a bird that arrives later clearly has fewer options to choose an early laying date than a bird that arrives earlier (Drent et al. 2003; Drent 2006). Further, assuming no strategic decisions, which means that prelaying periods are assigned randomly, all late-arriving birds would have a prelaying period that extends longer than the actual breeding season allows. These birds are either not sampled or would be forced to reduce their prelaying period to still be able to breed. Both would produce a bias in the data toward shorter prelaying periods for late-arriving birds, leading to an inherent dependence of A and D .

Thus, before thinking about strategic timing of migration and breeding, we need to confirm that birds indeed do strategically adjust timing of breeding according to timing of migration. We suggest that a correlation between any pair from arrival date, laying date, and prelaying period should be tested thoroughly to determine whether it is the result of intrinsic effects. More generally, for any two variables that are sequentially restricted, simple correlation or regression analyses are not sufficient to infer strategic behavioral decisions. Indeed, the statistical mis-

take that we report here has been made often, before and after the article we discuss here was published (e.g., Andersson and Gustafsson 1995; Potti 1999; Ahola et al. 2004). Not only in ornithology but also in the medical sciences, sequential variables are sometimes wrongly considered to be statistically independent (e.g., Blum et al. 2003).

One of several possible ways to test whether A and D , or A and L , are actually independent is via randomization. In this context, randomization is a useful method because it does not make a priori assumptions about the distribution of A or D . By randomizing pairings of A and D , one can construct the expected distribution of L under the assumption of independence. These data can be used to estimate the expected distribution of the preferred statistic (e.g., the correlation coefficient), against which the observed data can be tested. We think that the data presented by Bêty et al. (2003) could be used in this way to test the strategic reproductive behavior of migratory snow geese.

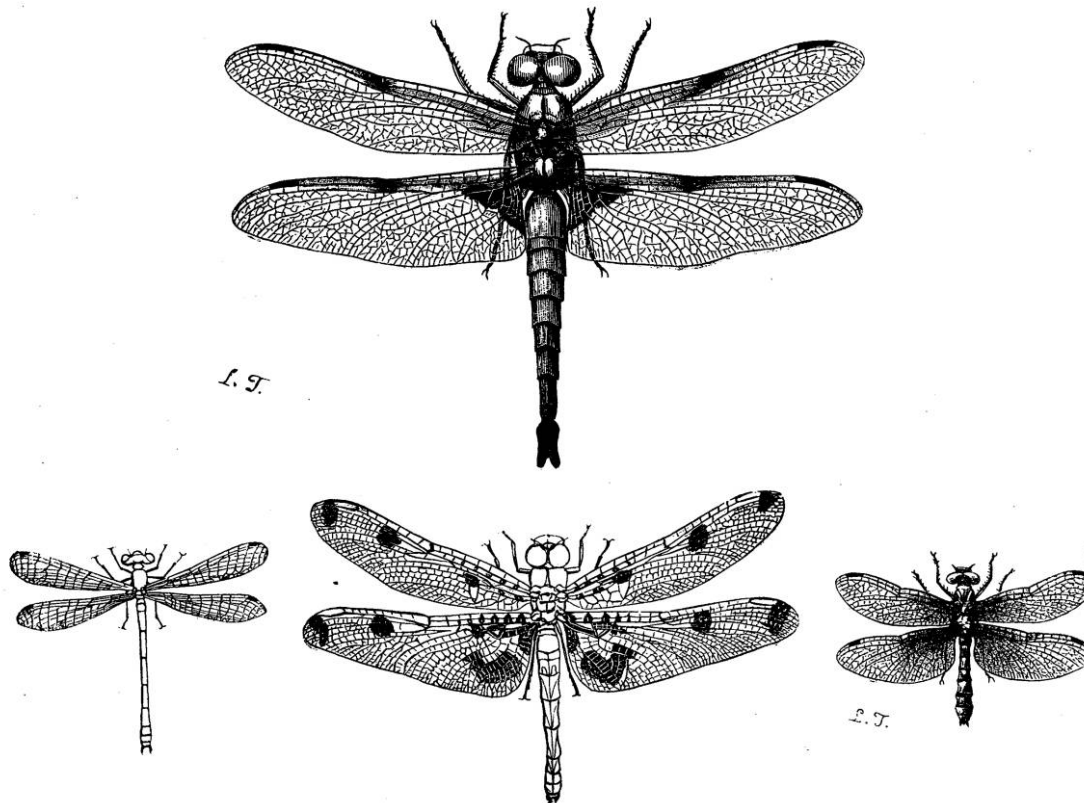
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Top, *Libellula quadrimaculata*, “the four-spotted Dragon-fly, seen on the wing in June, flying through dry pine woods.” Bottom left, *Agrion saucium*. Bottom center, *Diplax elisa*, “black, with the head yellowish and with greenish yellow spots on the sides of the thorax and base of the abdomen.” Bottom right, *Nannophya bella* female. From “The Dragon-Fly,” by A. S. Packard Jr. (*The American Naturalist*, 1867, 1:304–313).